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1 Network indicators of cultural resilience to anthropogenic removals in animal societies

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Abstract. Social learning, information transmission, and culture play vital roles in the lives of social animals, influencing their survival, reproduction, and ability to adapt to changing environments. However, the effect of anthropogenic disturbances on these processes is poorly understood in free-living animals. To investigate the impact of anthropogenic disturbance on social learning and information transmission, we simulated individual removal from contact networks derived from long-term behavioral datasets. We simulate the effects of individual removal on network efficiency and social learning for three group-living species – yellow baboons (*Papio cynocephalus*), African savanna elephants (*Loxodonta africana*), and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). We reveal how removals of key network positions reduce network efficiency. However, groups with high levels of innovation may cope with changing social network structures. These findings highlight the importance of protecting key individuals to preserve group structure and the role of innovation in possibly mitigating the fitness costs of removals. Identifying and safeguarding individuals that drive innovation can reduce a group's susceptibility to anthropogenic threats and promote cultural resilience in social animals in a changing world. These emerging trends contribute to a growing understanding of the role of conservation interventions in protecting critical individuals in group-living animals.

16 17 1. Introduction

18 For many species, group living has positive fitness consequences for individuals [1–3]. One
19 major benefit of group-living is that key information about resources [4], mates [5], predators
20 [6], and novel threats [7] may be gleaned socially through observation of, or interaction with,
21 another group member. Social learning may also contribute to the transmission of novel
22 behaviors, like the spread of novel foraging traditions or vocal repertoires. Socially-learned
23 foraging behaviors may propagate beyond an individual's immediate social group and transfer to

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24 other social groups when they come into contact [8]. For example, in humpback whales
25 innovative “lobtail” feeding behavior was spread via social transmission from a single whale [9]
26 and new vocal repertoires can rapidly emerge from song hybridization events [10]. Socially-
27 learned behaviors may also impact the survival and reproduction of individuals or in some cases,
28 entire social groups [11]. These traits can be particularly influential because they can spread
29 more rapidly within social groups than genetically inherited ones (i.e., within a single generation)
30 [12]. And, although culture was previously assumed unique to human societies [13], socially
31 learned and transmitted behaviors may contribute to group-specific, socially transmitted
32 traditions, or ‘animal culture’ [14,15].

33 Anthropogenic change can influence animal social dynamics. Evidence suggests that
34 humans can reduce opportunities for social learning and horizontal transmission of information
35 through the indirect reduction of group size associated with human presence [16] or via the direct
36 removal of key individuals from groups [17]. For example, chimpanzee communities in areas
37 with high human impact experienced an average behavioral diversity loss of 88% compared to
38 those residing in low-impact areas [18]. Moreover, among sperm whales, anthropogenic noise
39 reduces vocal communication [19] – a critical element of group cohesion [20]. In other cases,
40 however, social learning can help group-living animals cope with or even exploit anthropogenic
41 change. For instance, social learning promotes access to farmed foods by chimpanzees [21],
42 removal of fish from longlines by sperm whales [22], and opening of household waste bins by
43 cockatoos [23]. The emergence and spread of innovations vital to social learning can promote
44 adaptive responses to anthropogenic activities but also exacerbate human-wildlife conflicts.
45 Human disturbances, for instance, may also alter fundamental group structures [24], which may
46 lead to behavioral changes such as loss of vocal diversity in groups [25]. However, definitive
47 links between group structural features and behavioral repertoires are lacking and the social
48 mechanisms involved requires further study.

49 Social network analysis is a powerful tool for assessing how group structure shapes the
50 diffusion of social information and/or behavioral innovations within and across groups over time
51 [26,27]. Network analysis identifies key individual positions, such as those with many direct
52 connections (high degree centrality) or those that indirectly connect other individuals
53 (betweenness centrality) (e.g., [28]). For instance, in ravens simple exposure to new behaviors

54 does not guarantee social learning, and central individuals learn from and transmit information
55 among affiliates more rapidly compared to highly related or ranked individuals [29]. Network
56 analysis also describes overarching group structure through features like group density or
57 cohesion, nested hierarchical social levels, or modularity of subgroups [30]. Network
58 characteristics provide underlying structural conditions that influence the diffusion of socially
59 learned behaviors within social groups [31]. Removing an individual and their social connections
60 can have cascading consequences on the distribution of social connections among remaining
61 group members, affecting core processes within animal societies [32]. However, removal may
62 affect transmission differently depending on a given network's structural characteristics [33].
63 Building upon knowledge that disturbances (natural or anthropogenic) [34] shape animal social
64 structures, we simulated the consequences of human-induced removals on contact networks, and,
65 thus, the potential for social information transmission [32].

66 To gain insights into social learning dynamics and the potential for cultural transmission
67 across networks in nature [35], we leveraged data from long-term research projects on three
68 female-bonded social mammals: yellow baboons (*Papio cynocephalus*), African savanna
69 elephants (*Loxodonta africana*), and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*;
70 hereafter baboons, elephants, and dolphins). We chose these focal species due to: (1) the
71 hypothesized importance of social learning and cohesion in their social networks, (2) their
72 documented vulnerability to anthropogenic threats (i.e., poaching, bush meat, habitat loss,
73 disease), and (3) the availability of detailed long-term social data on these populations (for
74 details, see the electronic supplementary material).

75 Understanding the consequences of group structural changes – particularly following the
76 loss of individuals – on social information transmission could offer insights into species'
77 resilience to anthropogenic disturbance. Here, we investigate how social disruption affects group
78 structure by simulating removal of individuals of known ages and evaluating its impact on
79 inferred innovation rates. We first ask: (1) What are the defining structural features of each
80 network? With these metrics, we identify key individuals in social groups and ask: (2) How
81 efficiently can each group transmit social information (based on contact networks) across
82 members after key individuals are removed? And (3) what is each group's ability to solve
83 problems after individuals are removed?

84

85 **2. Methods**

86 **(a) Empirical study systems for characterizing social networks**

87 We used observational behavioral data for recognizable individuals belonging to known age
88 categories from three long-term field studies to compare the influence of group structure on
89 contact networks as a proxy for social learning (table S1).

90

91 **(i) Amboseli Baboon Project in Kenya**

92 East African baboons are highly cohesive social primates distributed across eastern and central
93 Africa [36]. Their groups (troops) are structured by linear dominance hierarchies and range in
94 size from less than 10 to nearly 200 individuals [37]. Social connections among females directly
95 influence fitness [1]. We used data on 55 females in one social group, collected by members of
96 the Amboseli Baboon Research Project between 1997 and 2001 (see [38] and its data). Group
97 size during this period of study had a mean of $23 \pm$ S.D. of 6 females (range: 15 to 32 females).

98

99 **(ii) Samburu Elephant Project in Kenya**

100 African savanna elephants have nested, multilayered (hierarchically structured), fission-fusion
101 societies [39]. Associations vary with resource availability: smaller, single matrilineal groups are
102 more common during dryer, resource-scarce periods, whereas larger herds of several hundred
103 individuals can occur when resources are abundant [40]. Social learning is common in elephant
104 societies with behaviors like crop-raiding learned from older individuals [41]. We used data on
105 201 female elephants from social networks with a mean $116 \pm$ S.D. of 17 females (range: 97 to
106 130 females) from the Samburu Elephant Project in Kenya's Samburu National Reserve
107 collected between 1998 and 2014 (for observation methods see [42]).

108

109 **(iii) Shark Bay Dolphin Research Project in Australia**

110 Indo-Pacific bottlenose dolphins are found in coastal waters throughout the western-Pacific and
111 Indian Oceans. These gregarious animals have regionally-variable social dynamics, with
112 individual-based fission-fusion behavior being a key characteristic (see [43]), and display
113 matrilineally-transmitted cultural behaviors including the use of marine sponges as foraging tools

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114 in a subset of the population [44,45]. We used behavioral data from juvenile (i.e., weaned
115 individuals, typically 4-10 years of age, N = 23) and adult female dolphins (>10 years, N = 155)
116 from the Shark Bay Dolphin Research Project in Shark Bay, Australia [46] collected during boat-
117 based surveys between 2008 and 2019 comprised of 178 unique females with network sizes
118 ranging from 102 to 150 females (mean $132 \pm$ S.D. 18 females).

119

120 **(b) Network construction for cross-species comparisons**

121 To facilitate cross-species network comparisons, we accounted for variable data
122 collection and different life histories by dividing the data into discrete “waves” of one, two, or
123 three-year intervals for baboons, dolphins, and elephants, respectively (table S1). This allowed us
124 to normalize lifespan differences and encompass the timescale necessary to capture temporal
125 variation within groups. Within each wave, species-specific associations or affiliative
126 interactions between individuals were represented as undirected, symmetric ties (see the
127 electronic supplementary material). To control for sex-based social segregation [43], we focused
128 only on social associations among females in each social network. Among mammals, females
129 often play a central role in passing on social and ecological information to offspring and other
130 group members [47]. More generally, the processes influencing social learning in males and
131 females are expected to differ because of sexually dimorphic social constraints and therefore
132 require sex-specific study [48]. Our work also extends previous studies focused on male
133 removals (e.g., via trophy hunting [49,50]). Therefore, understanding the effects of female
134 removals should offer important insights into the conservation of animal behavioral repertoires.

135 To quantify the effects of various individual removal scenarios on group social-cultural
136 transmission, we 1) described network structural features for each species, 2) tested the
137 efficiency of within-wave information diffusion as a simple proxy for information transmission,
138 3) assessed group performance by simulating more biologically nuanced scenarios of
139 information transformation via individual social learning and innovation. For step two, we
140 compared the undisturbed group to random, age-based, and key position-based removal
141 scenarios. For step three, we compared the undisturbed group to random and age-based removal
142 scenarios. All analyses were done in R version 4.1.2 [51].

143

144 (c) Modeling network structural features

145 We modeled independent weighted social networks for each species and wave using the *igraph*
146 package [52]. In these networks, ‘nodes’ represent individuals that associate with each other via
147 ties; interactions between individuals are weighted by interaction frequency (species specific
148 details above). From each network, we extracted individual-level degree and betweenness
149 centrality, which indicate an individual’s importance in a group for facilitating information
150 transmission. We then calculated five network structural features that could influence
151 information transmission: modularity, transitivity, density, average degree (number of nodes),
152 and average weighted path length (table 1) [30,53].

154 (d) Efficiency as a proxy for information transmission

155 To conceptualize capacity for each animal group to socially transmit information via member
156 contact networks, we examined the efficiency of potential information spread between members.
157 Here, efficiency is inversely proportional to the weighted path length between nodes and
158 describes the potential for between-node communication [54]. This pairwise definition of
159 efficiency can be expanded to describe the overall network efficiency as the sum of all inverse
160 path lengths between node pairs. Efficiency will be higher in a network with shorter path lengths
161 between nodes. The removal of individuals could affect the average length of paths in the
162 network, thus affecting the structure’s ability to transmit information.

163 We first evaluated the potential efficiency of information diffusion for each wave of our
164 three species’ networks (i.e., no removals). We then examined the effects of several types of
165 individual removal – random, age-based, and key position-based (degree or betweenness
166 centrality) – on potential efficiency. Random removal served as both a baseline to understand the
167 impact of any type of removal and a way to understand resilience to opportunistic hunting. Age-
168 based removal maps most closely to expectations of natural death, including the possibility that
169 the oldest individuals are most vulnerable to disease and to trait-based hunting (e.g., for elephant
170 tusks). We also modeled the effects of losing individuals occupying key network positions (e.g.,
171 high degree, betweenness centrality) on group efficiency.

172 When simulating group member loss we used a stepwise approach, removing one percent
173 of nodes per wave at a time. This gradual removal of individuals continued until 20% of

174 individuals were removed. Then, to assess the impact of these removals on the network's
175 efficiency, we compared network efficiency at each removal step to that of the intact network.
176 Specific to random removal, we repeated the process of removal and efficiency calculation 100
177 times to account for the inherent variability resulting from random removals [55]. Finally, the
178 efficiency values from the repeated random removal simulations were averaged to provide a
179 more robust representation of the network's efficiency throughout the removal process.

180

181 (e) Social learning and innovation on fitness landscapes

182 We next evaluated groups' ability to solve problems by comparing simulations of individual
183 social learning and innovation before and after random and age-based removals. We used this
184 approach to provide a more nuanced understanding of social learning across different innovation
185 levels to acknowledge that exposure to social partners does not ensure social learning and to
186 explore transmission of cultural variants of different utility. Specifically, we (i) used an NK
187 model, which simulates a theoretical rugged fitness landscape (hereafter fitness landscape) where
188 higher "elevation" represents innovation of more advantageous behaviors or acquisition of
189 information leading to increased fitness outcomes. In the model structure, we (ii) included age-
190 based rules to account for three potential biological scenarios: certain individuals are more likely
191 to innovate than others, older individuals have more successful behaviors (e.g., acquiring
192 resources, accessing social benefits, etc.), and individuals learn via age-ranked transmission (i.e.,
193 from older individuals, not exclusively from parents). (iii) We used a range of innovation
194 probabilities for each removal type to account for variable innovation rates. (iv) Lastly, the
195 simulations included a series of timesteps wherein individuals explored the fitness landscape
196 (innovate) and observed each other (socially learn). At each step, individuals (agents), only
197 moved to a position – learned either socially or through innovation – if it was higher (more
198 advantageous) in the fitness landscape. The simulations, then, reflect how the species' networks
199 can find the peaks in the rugged landscape, indicating learning that improves fitness, and how
200 this search is potentially affected by varying innovation rates and different types of removal (see
201 the electronic supplementary material).

202

203 (i) Simulating social learning strategies on fitness landscapes

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204 We simulated problem-solving tasks to evaluate how social learning strategies of individuals
205 influence group performance on a rugged fitness landscape. Since their introduction, rugged
206 landscapes have been widely used to represent complex problem spaces [56] and examine how
207 individuals within specific social structures can collaborate to solve such problems [57]. Within
208 the landscape, higher positions represent solutions with increased fitness pay-offs (i.e., a better
209 solution). Here we generated a rugged fitness landscape (i.e., with multiple adaptive peaks, each
210 with a local optimum) using an NK model [57]. In this landscape, N refers to the number of
211 elements in a solution whereas K refers to the interrelationships among these elements. Together,
212 these were used to define the structure of the problem-solving task and the fitness payoff of each
213 solution by including 2^N potential positions in the fitness landscape and K ruggedness. In the
214 simplest case for NK models ($K = 0$), there is a single peak; in the most complex case ($K = N -$
215 1), the landscape is dominated by multiple uncorrelated peaks. In other words, when K is low,
216 the outcomes of innovation are straightforward – the height of the current position is highly
217 predictive of the benefits to be gained in adjacent positions. When K is high, however, positions
218 are uncorrelated, so each step might entail substantial changes in height. This could lead
219 individuals to a local maximum rather than an overall optimal solution, thus making new
220 strategies risky. We created a moderately-complex landscape with $K = 6$ and selected $N = 12$
221 positions in the landscape. This yielded 4,096 potential positions available to individuals in the
222 network – many more possible positions than individuals in the network (see the electronic
223 supplementary material).

224

225 (ii) Social transmission across innovation scenarios

226 We created a series of biologically based rules for how transmission of information within each
227 innovation scenario can occur. Potential starting positions, equal to the number of individuals per
228 wave, were randomly selected from the 4,096 potential fitness landscape positions. Older
229 individuals were placed in higher quality positions, reflecting the assumption that age correlates
230 with beneficial behaviors linked to survival. While high starting positions confer initial
231 advantages, they could also result in individuals getting stuck at local optima because their
232 positions are higher than the immediate vicinity but not the high points in the whole landscape.
233 Such a pattern reflects a biological possibility where older, moderately successful individuals are

234 less likely to seek newer, better strategies (e.g., dolphin tool use; [58]). Additionally, we
235 stipulated several rules for the social transmission of information via vertical learning.
236 Specifically, individuals could (i) learn from better-positioned, older ties in their network at (ii) a
237 probability equal to the relative weight of their tie to (iii) increase their fitness outcome from the
238 acquisition of this knowledge [14]. For example, dolphin tool use is vertically transmitted from
239 mother to primarily female offspring via social learning [59] with individual fitness
240 consequences [60]. Thus, we assumed individuals would only move to a new position (through
241 social learning) if this represented an increase in fitness. The rules above were applied to three
242 currently debated innovation scenarios: younger individuals are more likely to innovate (young
243 innovate) [61]; older individuals are more likely to innovate (old innovate) [62]; or, both young
244 and old innovate (all innovate) [63]. For the innovation scenarios, we categorized individuals
245 into two age classes, "younger" and "older," based on whether they were below or above the
246 species' maximum peak reproductive age (baboons = 14 yrs, elephants = 40 yrs, dolphins = 25
247 yrs) [58,64,65].

248

249 (iii) Modeling how innovation rates moderate the effects of removals

250 For each innovation scenario, we tested how innovation rates, modeled as the probability of
251 innovation π , moderate the effects of removal. At low values of π , indicating little innovation for
252 new strategies, we expected age-based removal to harm the networks as there is little learning,
253 making the accumulated knowledge (higher starting positions) of older individuals more
254 important. At higher probabilities of innovation, however, older individuals that cannot learn
255 might lower the average group performance of a population that continuously innovates. We
256 explored values of π from 0 to 0.2 in increments of 0.02. These values reflect an extreme range
257 of potential proportions of an individual's time spent innovating, while acknowledging that – due
258 to the error-prone nature of innovation – social learning remains the dominant strategy. For each
259 value of π within each removal scenario, we ran 100 simulations.

260

261 (iv) Simulating the effects of age-based innovation on fitness

262 We ran 100 simulations at each innovation rate (enough time for the group response to reach an
263 asymptote). At the start of each simulation, individuals were seeded following the rules for

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264 vertical transmission (see section ii). Then, for each removal scenario, no individuals
265 (undisturbed), a random 10% of individuals (random removal), or 10% of the oldest individuals
266 (age-based removal) were removed. We chose 10% removal because it doubles the average
267 annual adult mortality for baboons [66], dolphins [67], and elephants [68], which we would
268 expect to have a significant impact on each population. The model was then run for 500
269 timesteps, at the end of which, the average fitness (height of all individuals) of the wave was
270 recorded. Within each age-based innovation scenario, models adhered to the following rules at
271 each timestep: (1) “innovators” had π probability of exploring one adjacent position. (2)
272 However, individuals that explored an adjacent position only moved to that new position if doing
273 so increased their fitness payoff. (3) Although “non-innovators” were not permitted to explore
274 adjacent positions, if they were directly connected to at least one individual older than
275 themselves then they could increase their fitness via social learning if they observed a position
276 higher than their current one. Non-innovators socially learned from their older connection with
277 the best position with a probability equal to the weight of their tie. (4) Thus, the fitness of non-
278 innovators also never decreased across time steps but could increase for those individuals
279 directly connected to better-connected, older individuals (i.e., if they learned via transmission of
280 information directly from associates older than themselves).

281

282 **3. Results**

283 **(a) Social network structural features**

284 Although between-species statistical comparisons of network structures remain a major
285 challenge in the study of animal social networks [30], our simulations offer preliminary insights
286 into network features for each of the three species at multiple time points. Across waves ($n = 6$),
287 baboon networks had an average of 23 (+/- 5 SD) individuals and 113 (+/-40 SD) ties (table 1;
288 figure S1). While baboon networks were smallest of the three species, their transitivity, density,
289 and average path length were between those of dolphin and elephant networks. Elephant
290 networks had an average of 116 (+/- 14 SD) individuals across waves ($n = 3$) and 4,920 (+/- 959
291 SD) ties. The considerable number of ties relative to individuals is likely due to large social
292 groups formed during the wet season when resources are abundant [40,69]. Of the three species,
293 elephant networks tended to have the most ties, be the densest and the most transitive, and,

294 finally, had the smallest average path length between the individuals. Lastly, dolphin networks
295 had an average of 132 (+/- 16 SD) individuals across waves (n = 6) and 796 (+/- 224 SD) ties.
296 Their networks were the least dense, least transitive, most modular, and had the largest average
297 path length between individuals.

298

299 **(b) Efficiency as a proxy for information transmission**

300 Prior to individual removal, the potential efficiency of the baboon, elephant, and dolphin
301 networks averaged 0.401 (+/- 0.069 SD), 0.493 (+/- 0.010 SD), and 0.298 (+/- 0.069 SD),
302 respectively across waves (figure 2). Age-based and random removals had a similar near zero
303 effect on efficiency (figure 2). Removal of key individuals, measured by degree or betweenness
304 centrality, reduced group efficiency more than random or age-based removals (figure 2). In
305 general, the baboon and dolphin networks displayed a greater efficiency loss after removals than
306 the elephant networks.

307

308 **(c) Simulating information transmission**

309 We simulated information transmission under three innovation scenarios: (i) both young and old
310 individuals innovate (all innovate), (ii) only young individuals innovate (young innovate), and
311 (iii) only old individuals innovate (old innovate). Here, we focus on the results of the all-
312 innovate scenario. We then share case-specific results from the young innovate and old innovate
313 analyses when they differ from the all-innovate scenario. Results of each simulation timestep are
314 reported as the difference in average group fitness between the no-removal baseline and removal
315 scenario. Negative values indicate reduced fitness relative to no removal scenarios. Conversely,
316 positive values represent higher overall fitness compared to the scenario without any removals.

317 *All innovate scenario.* In most waves across species, when all individuals innovate, both
318 random and age-based removal resulted in a negative difference in mean fitness (i.e., reduced
319 fitness, on average; subset in figure 3; full results in figure S2). For innovation rates greater than
320 zero, this negative difference is characterized by a steep initial decrease in fitness. In addition,
321 across timesteps within and across rates of group innovation (π), both random and age-based
322 removal showed similar decreasing gaps in fitness compared to no removal. For both removal
323 scenarios, when the rate of innovation was low, removal tended to have a greater negative effect

324 on average fitness. As innovation rate increased, the difference in fitness between removal and
325 non-removal scenarios approached zero.

326 We found species-specific trends in the difference in mean fitness from the non-removal
327 baseline following random and age-based removal (figure 3A). When all individuals innovated,
328 the initial difference in mean fitness between removal and non-removal scenarios and recovery
329 across timesteps was similarly small for baboons and elephants. After completion of all
330 timesteps, removals had negligible fitness consequences for elephants and baboons, and the
331 differences in fitness for both age-based and random removal scenarios generally reached zero
332 for the simulations. The fitness gap did not close as quickly or become as small across timesteps
333 and innovation rates for dolphins.

334 *Young innovate scenario.* The most notable difference between the young innovate and
335 all innovate scenarios is the wider gap between random and age-based removal across timesteps
336 and innovation rates (figure 3B). Unlike the all innovate scenario, the young innovate scenario
337 with random removal consistently generated greater negative differences in mean fitness (i.e.,
338 reduced fitness) than age-based removals. Contrasting the other innovation scenarios for
339 elephants, waves wherein young innovate generally maintained the greatest negative difference
340 in mean fitness between random removal and non-removal and the greatest positive difference in
341 mean fitness between age-based removal and non-removal across timesteps and rates of
342 innovation. In some dolphin waves under the young innovate scenario, random removal
343 increased negative differences in mean fitness across timesteps.

344 *Old innovate scenario.* Under the old innovate scenario, age-based removal generated
345 negative differences in fitness greater or equal to that of random removal (figure 3C). This was
346 particularly true for baboons where age-based removal generated increasingly negative
347 differences in mean fitness with greater rates of innovation. For baboons and dolphins, greater
348 rates of innovation generally had less effect on the difference in mean fitness compared to young
349 innovate and all innovate scenarios.

350

351 **4. Discussion**

352 **(a) Network structural features vary with social cohesion**

353 We used long-term data for three focal species to construct networks representing three levels of
354 female social cohesion in animal social groups. We then derived commonly used network
355 properties to determine the features most influential for social learning and information
356 transmission. We found several major differences in the underlying network features across
357 species and waves, which we attribute to variable species social dynamics.

358 First, across seasons, elephant networks were large and dense with many connections
359 between individuals rather than separate subgroups. This elephant network structure was likely
360 facilitated by the abundance of wet season resources, which can promote social cohesion [39]. In
361 contrast, resource scarcity promotes preferential associations with kin, leading to hierarchical
362 structures that result in periods of clustered elephant subgroups [70]. Dolphin networks were the
363 least dense, least transitive, most modular, and had the longest average path length between
364 individuals. These dispersed networks with clustered subgroups resulted from individual
365 dolphins temporarily separating from the group to avoid foraging or social competition [71,72].
366 Baboon networks were the smallest, but their transitivity, density, and average path length were
367 in between those measures for dolphin and elephant networks. Because of their constant
368 proximity and low social tolerance, baboon preferential affiliations are likely responsible for
369 these structural features [73].

370

371 **(b) Network efficiency harmed by loss of key network positions**

372 We calculated network efficiency before and after individual removals [54]. Before removals,
373 elephant networks had the highest efficiency of the three species, indicating that information
374 transmission is likely more effective and resilient in elephant networks than the other study
375 species. We attribute this, in part, to the high density and low modularity of elephant networks
376 aggregated across seasons. Rather than a few subgroup-spanning individuals creating pinch
377 points for information diffusion, individuals were connected through multiple pathways across
378 seasons, creating more redundancy (resilience) for information flow. Elephants' high mobility,
379 which reduced observation frequency, necessitated aggregation of association data at a coarser
380 temporal scale than dolphins and baboons. This likely inflated elephant network density
381 calculations, which could explain why removals had a smaller effect on network efficiency for
382 elephants than baboons and dolphins. That said, high-density aggregations in the wet season are

383 characteristic of elephant social behavior and explain high network efficiency for elephant
384 networks [69].

385 Despite living in permanent social groups, baboon waves had moderate network
386 efficiency relative to elephants and dolphins. This efficiency may reflect baboons' low social
387 tolerance, which results in distinct preferences for social partners with whom they share
388 information [3,73]. Consequently, most learning and information transmission occurs through
389 preferred affiliates [74], especially among younger individuals [75]. Despite this, we expected
390 some learning from all individuals in the group as they are often in visual proximity. This
391 affiliate-specific information pipeline results in little or no flow of information across subgroups.
392 As such, it is important to note that our values for baboon network efficiency may reflect the
393 biological reality of low social tolerance as well as the practical need for a more nuanced
394 proximity metric that accounts for permanent group residence.

395 All three species experienced the greatest reduction in network efficiency following the
396 removal of individuals in key network positions as compared to random and age-based removals.
397 Despite removing up to 20% of individuals for random and age-based removals, efficiency
398 stayed relatively constant, indicating that social groups are generally robust to the loss of older or
399 less socially central individuals. This pattern underscores that important roles are not always
400 linked to biological traits but are part of a complex interplay between network position and social
401 influence in collective decisions [29,76–78]. Importantly, the network structure underlying group
402 member affiliations may be key for ensuring the resilience of information transmission in the
403 face of anthropogenic removal. More generally, it will be important to understand whether
404 individuals with important network positions are also more vulnerable to human-induced
405 mortality, and, if so, the extent to which these costs overwhelm positive links between sociality
406 and longevity across taxa in many social mammals (e.g., killer whales [79], baboons [3],
407 elephants [80]).

408 Overall, the loss of a greater number of individuals led to a greater decrease in efficiency;
409 however, the severity of decrease in their networks' efficiency varied by species and their
410 network structural features. Although methodological advances are needed to explicitly examine
411 inter-specific differences in network characteristics influencing information transfer, our data
412 offer preliminary evidence for each of the focal populations in this study. From a structural

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413 perspective, networks with low density, high modularity, and long average path lengths (i.e.,
414 dense connections within subgroups but sparse inter-connections between them) are particularly
415 susceptible to individual removal. For example, dolphin groups, which have the highest average
416 path length, lowest density, and high modularity across waves, consistently had the greatest loss
417 of efficiency with the removal of individuals in key network positions. Compared to dolphins,
418 baboons and elephants have similar levels of modularity, but elephant group were denser, with
419 more ties between individuals, which made it easier for elephants to maintain capacity for
420 transmission through interconnected network structure despite individual loss. .

421 The resilience of elephant and baboon efficiency (following individual loss) seen in our
422 study aligns with previous observations connecting the role of key network positions and
423 network structure to cultural resilience in these species. Strong kin-biased associations among
424 elephants [81] may contribute to the ability for elephants to maintain the transfer of information
425 despite loss. For example, if an elephant matriarch dies, her equally well-connected daughter
426 replaces her in the group [82]. Whereas, if an important female baboon dies, multiple individuals
427 with weaker ties collectively compensate for her loss [83]. In contrast, dolphins' foraging
428 innovations primarily transmit vertically through matriline with some behaviors exhibited by
429 only one female and her descendants [84]. Consequently, the loss of one individual could
430 eradicate a particular foraging tactic. For example, dolphins that use sponge tools represent only
431 5% of the population [85], so removal of a few individuals could mean the loss of the behavior.
432 Moreover, because foraging is usually a solitary activity, there is a low probability of
433 transmission except within matriline, especially for rare tactics [85]. The apparent role of low
434 modularity in maintaining network efficiency provides a starting point for a networks-based
435 approach identifying groups of a species that are most vulnerable to loss of cultural variants.

436

437 **(c) Innovation recovers fitness benefits of social learning**

438 To go beyond efficiency, a static estimate of social learning, we simulated generic problem
439 solving in a theoretical "rugged landscape" and compared group responses in removal and non-
440 removal scenarios. Across age-based and random removals, removals universally reduced mean
441 fitness regardless of species, innovation scenario, or innovation probability. Although the loss of
442 individuals initially fractured network connections and reduced opportunities for social learning,

443 innovation was the driving force behind recovery of group fitness over time. In other words,
444 greater innovation appeared to increase exploration for previously unknown solutions with
445 higher fitness pay-offs over favoring known solutions with lower pay-offs stemming from older
446 individuals [86]. In almost all waves, increasing the rate of innovation led to an improvement in
447 overall group fitness because novel solutions could emerge that were not inhibited by broken
448 network connections or by older individuals teaching suboptimal problem-solving techniques.
449 However, in situations where there were no or very few individuals capable of innovating,
450 increasing the innovation rate did not improve fitness and, in some cases, widened the gap in
451 fitness between removal and non-removal groups over time.

452 Without the introduction of innovations, connected individuals quickly transferred
453 existing information, leaving the difference in group fitness static. The growing gap between
454 baseline and removal groups, where essentially one group is innovating and the other is not,
455 highlights the potential value of innovation in group recovery after disturbance. While the role of
456 innovation in facilitating group recovery after disturbance has not yet been studied, our findings
457 are in line with evidence suggesting that innovation leading to behavioral diversity enables
458 species to exploit new niches [87]. Nonetheless, although our results are consistent with
459 theoretical and empirical expectations of social learning, our models were not designed to fully
460 capture the potential costs of “bad” innovations and future work should do so.

461 Removal had a disproportionately negative effect on group fitness when removal targeted
462 the innovator group. In waves where all individuals innovated, we saw similar trends of a
463 shrinking gap in mean fitness for both removal scenarios, because innovators were removed in
464 both scenarios. This mirrors our findings regarding the effects of removal on efficiency, whereby
465 random and age-based removal had a similarly small effect. The effect of random removal on
466 group fitness when only young individuals innovated was greater than the effect of age-based
467 removal on group fitness when only old individuals explored. These findings inform recent
468 debates [61–63] about the importance of young versus older individuals in innovating solutions.

469

470 **5. Implications for culture conservation**

471 Across species, many groups experience losses that start with the gradual reduction of group size
472 and result in increased risk for an “extinction spiral” [88]. Given the increasing threat of human-

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473 driven removals of animals from their social groups, it is crucial to consider and implement
474 effective interventions that can support the resilience in animal societies to reduce further
475 negative fitness consequences. Although social animals have evolved adaptive responses to cope
476 with the loss of specific associates [83,89], the current magnitude of anthropogenic impact is
477 outpacing evolved responses [24], resulting in the disruption of social groups. Our study
478 demonstrates the negative effects of these removals across multiple taxa, but also suggests that
479 social groups can display a surprising amount of resilience to loss, especially when the loss
480 follows a predictable pattern, such as the loss of old individuals, and when rates of innovation are
481 high. These findings extend previous research describing several adaptations to the loss of group
482 members, including group policing to enforce diverse interactions between group members or
483 equally well-connected offspring after the loss of a parent [82,90]. More broadly, these patterns
484 underscore the emerging idea that animal social structures, including social connections [32] and
485 social information [91] – that together contribute to animal culture [11] – can play a vital role in
486 the conservation of social species.

487

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